

A REVISION OF THE LAKE VICTORIA HAPLOCHROMIS SPECIES (PISCES, CICHLIDAE)

PART II¹: *H. SAUVAGEI* (PFEFFER), *H. PRODROMUS* TREWAVAS, *H. GRANTI* BLGR. AND *H. XENOGNATHUS*, SP. N.

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¹ Part I, see Greenwood, 1956b.

INTRODUCTION

MORPHOLOGICALLY, the *H. sauvagei* complex stands apart from any other species-group in Lake Victoria. The principal group character is that of the dentition which combines recurved outer teeth with multiserial inner tooth-bands (Text-fig. 3).

Furthermore, the shape of the neurocranium, although differing intra-specifically within the group, is unlike that of other *Haplochromis*. This character is probably associated with the multiserial dentition and relatively powerful jaw musculature. Indeed, amongst the non-piscivorous predators such marked divergence in cranial anatomy is otherwise only found in mollusc-eating species with hyper-developed pharyngeal bones and musculature. Two specifically constant forms of neurocranium occur in the "*sauvagei*" group, but neither can be correlated with the type of dental pattern present.

Trophically, members of the group may be classed as mollusc eaters, although available data indicate that other food organisms do contribute to their diet, usually in a subsidiary capacity. Unlike other mollusc-eating *Haplochromis* in this lake, species of the "*sauvagei*" group do not swallow the shells of their prey, but remove the soft parts before ingestion takes place. In this respect the feeding method is like that of *Macropleurodus bicolor* (Blgr.), a monotypic genus apparently derived from this group.

***Haplochromis sauvagei* (Pfeffer), 1896**
(Text-fig. 1 and Pl. 1 upper fig.)

Ctenochromis sauvagei Pfeffer, 1896, *Thier. Afr. Fische*, 15.

Haplochromis nuchisquamulatus (part), Boulenger, 1915, *Cat. Afr. Fish.*, 3, 290.

Paratilapia granti (part), Boulenger, 1915, *op. cit.*, 342.

Paratilapia bicolor (part) Boulenger, 1915, *op. cit.*, 346.

Paratilapia retrodens (part), Boulenger, 1915, *op. cit.*, 235.

Haplochromis sauvagei (part), Regan, 1922, *Proc. zool. Soc., Lond.*, 167.

? *Paratilapia crassilabris* (part), Boulenger, 1915, *op. cit.*, 345.

I was unable to examine the holotype of *H. sauvagei* which was mislaid during the 1939-45 war; at present the Berlin Museum authorities cannot confirm whether this specimen has been lost. Pending more definite information, no neotype can be selected, but, should such a step become necessary, I suggest that the specimen B.M. (N.H.) Reg. No. 1956.9.17.1, a male from Entebbe (Text-fig. 1) be given neotypical status.

Fortunately, Pfeffer's original description of *Ctenochromis sauvagei* is comprehensive, and, when coupled with a photograph of the type, clearly indicates to which *Haplochromis* species his specimen should be referred. The photograph, preserved in the British Museum (Natural History), is reproduced in Plate 1.

Additional material discloses only one important discrepancy with the original description, in which the mouth and lower-jaw profile are described as rising steeply: ". . . ; das untere Profil der Unterkinnlade steigt viel stärker. Die von dicken und breiten Lippen umgebene kurze Mundspalte steigt nach vorn sehr steil auf."

In most specimens the ventral head profile is almost horizontal, or, at most, slightly oblique. A possible explanation for this discrepancy may lie in the fact that Pfeffer's description was taken from a fish preserved with its mouth open. From the photograph it is clear that, if the jaws were restored to their natural position, the cleft and lower jaw profile would be slightly oblique.

The present synonymy for *H. sawagei* is essentially that prepared by Regan (1922), but some of the specimens which he referred to this species are now placed in others. In this connection, reference should be made to the list of study material.

Paratilapia crassilabris part (Boulenger, 1915) is tentatively retained in the synonymy on the basis of a single specimen (B.M. (N.H.) Reg. no. 1911.3.3.32). This individual cannot be identified with certainty, but it is nearer *H. sawagei* than any other species with thickened lips and dentition not of the generalized type.

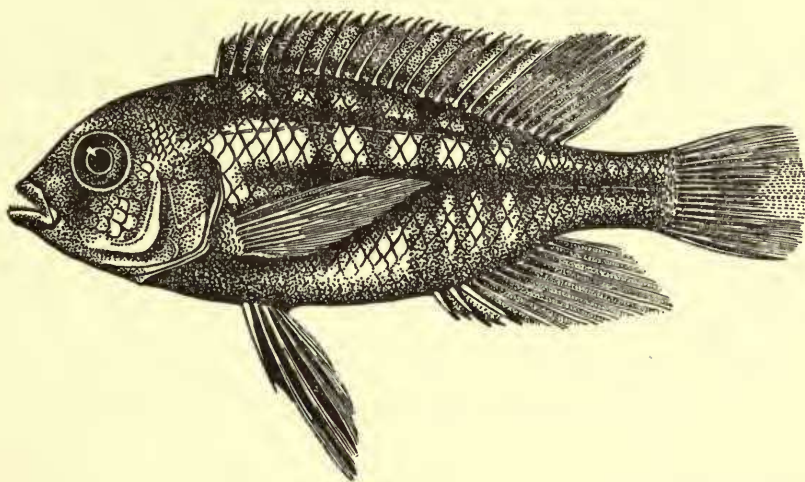


FIG. 1. *Haplochromis sawagei*, ♂, B.M. (N.H.) 1956.9.17.1. Drawn by Miss L. Buswell.

Description. Based on 85 specimens, 58–105 mm. standard length. Of the measurements made, only cheek depth clearly shows allometry with standard length.

Depth of body 30.4–41.8, mean (M) = 35.6; length of head 29.6–34.5 (M = 31.9) per cent of standard length. Dorsal head profile varying from decurved to straight, but strongly sloping, the former shape occurring more frequently.

Preorbital depth 15.4–20.2 (M = 17.3) per cent of head length, least interorbital width 23.0–31.2 (M = 27.0) per cent. Snout as broad as long, its length 27.2–35.5 (M = 30.8) per cent of head; eye diameter 25.7–33.4 (M = 28.9) per cent. Cheek becoming relatively deeper with increasing standard length; four size-groups are recognized, 58–69 mm. S.L. (N = 13), 70–80 (N = 21), 81–90 (N = 27) and 91–105 (N = 24), for which the cheek depth is 21.0–25.0 (M = 23.2), 20.4–26.0 (M = 23.7), 22.0–26.9 (M = 24.4) and 24.1–26.6 (M = 25.1).

Caudal peduncle 13.9–19.3 ($M = 16.4$) per cent of standard length ; its length 1.1–1.6, times its depth.

Mouth horizontal or slightly oblique ; posterior maxillary tip reaching or almost reaching the vertical to the anterior orbital margin. Lips thickened ; the depth of the upper lip, measured mid-laterally, is contained 4–4½ times in the eye-diameter. Jaws equal anteriorly, the lower 30.6–37.7 ($M = 34.5$) per cent of head length and 1.0–1.5 (mode 1.3) times as long as broad.

Gill rakers short, 7–9 (rarely 10) on the lower limb of the first arch.

Scales ctenoid ; lateral line with 31 (f.7), 32 (f.29), 33 (f.39), 34 (f.9) or 35 (f.1) scales ; cheek with 3–4 (rarely 2) series. 7–9 (less frequently 6) scales between dorsal fin origin and upper lateral line ; 7 or 8 (less commonly 6 or 9) between pectoral and pelvic fin-bases.

Fins. Dorsal with 24 (f.11), 25 (f.56) or 26 (f.18) rays, anal 10 (f.1), 11 (f.10), 12 (f.71) or 13 (f.3), comprising XV–XVII, 8–10, and III, 7–10 spinous and branched rays for the fins respectively. Pectoral slightly shorter than the head, or occasionally of equal length. Pelvic with the first ray produced, variable in its posterior extension but longer in adult males than females. Caudal sub-truncate.

Lower pharyngeal bone triangular, its dentigerous area 1½–1¼ times as broad as long ; pharyngeal teeth slender and cuspidate. In some specimens, teeth in the median rows are slightly enlarged, but retain their bicuspid crowns.

Teeth. In the outermost series of both jaws, the teeth have strongly recurved tips and are unequally bicuspid or unicuspid. The predominant tooth form is apparently correlated with length. Fishes less than 80 mm. S.L. have mainly bicuspid teeth, those in the range 80–90 mm. have either unicuspid or an admixture of uni- and bicuspid, whilst larger individuals possess mainly unicuspid teeth. When both types of teeth are present, the unicuspid form usually occurs anteriorly and laterally. There are 32–56 (mode 42) outer teeth in the upper jaw.

Inner teeth are either tri- or unicuspid ; as in the outer series, unicuspid teeth are commoner in fishes above 80 mm. S.L. Antero-medially, the teeth are arranged in a broad band comprising 3–8 (mode 4) and 2–6 (modes 3 and 4) rows in the upper and lower jaws respectively. Laterally, the band narrows to a single series. A distinct inter-space separates the inner and outer series.

Syncranium and associated musculature. Neurocranial form in *H. sauvagei* departs quite considerably from the generalized *Haplochromis* type, and approaches that of *Macropleurodus bicolor* (Greenwood, 1956a). Essentially the same points of difference with the generalized type occur in both species. The skull has a fore-shortened appearance due to the strongly decurved and almost vertically disposed ethmovomerine region. This curvature affects the morphology of the entire pre-orbital skull which is less gently curved than in the generalized neurocranium.

On the other hand, the jaws do not exhibit such radical departure from the generalized condition. The premaxilla, apart from a slight broadening of its dentigerous area, compares closely with that of other *Haplochromis* ; the dentary is somewhat shorter, more massive and has a wider median dentigerous area than is common in generalized species. Consequent upon these modifications slight differences are apparent in the suspensorium.

Muscle disposition and form are similar to those of basic *Haplochromis* species. However, the *adductor mandibulae* I is slightly longer (38–44 per cent head length compared with 36–39 per cent) and broader (length/breadth ratio 3.0–3.7 cf. 4.4–5.5).

The syncranium, its musculature and the dentition all foreshadow the condition found in *H. prodromus*, and therefore that which reaches its ultimate expression in the genus *Macropheurodus* Regan (Greenwood, *op. cit.*). It is perhaps significant that variability in the degree to which the syncranium departs from the basic type is greater in *H. sauvagei* than in *H. prodromus*.

Causal factors responsible for the characteristic preorbital face in both *H. sauvagei* and *H. prodromus* are not readily determined. From an examination of larval fishes it is manifest that, as in *M. bicolor*, this form develops during post-larval ontogeny. It is probably effected by differential growth of various syncranial parts, especially since the ethmovomerine region is not directly affected by the moulding influence of muscle insertions. However, the premaxilla, which is closely associated both anatomically and functionally with the dentary, could exert considerable influence over this region. In *H. sauvagei* the dentary is short in relation to the head and also in comparison with other *Haplochromis* species of comparable size. If, during post-larval ontogeny, this bone increased in length more slowly than the neurocranium, and if it is to remain functionally integrated with the upper jaw, then there can be two morphological results: either a skull of the *H. sauvagei* type, or one in which the upper jaw projects anteriorly beyond the lower. A third possibility, that the suspensorium be rotated anteriorly, cannot be considered in this case, since its almost vertical alignment in *H. sauvagei* is typically that of the basic type.

H. sauvagei includes Gastropoda as a substantial part of its diet. As in *H. prodromus* and *M. bicolor* the soft parts alone are ingested. The feeding habits of *M. bicolor* have been described elsewhere (Greenwood *op. cit.*): when feeding on snails, aquarium-kept *H. sauvagei* follow the same general pattern, except that after grasping the foot of the snail between its jaws the fish then uses the shell as a fulcrum to lever out the soft parts. Only rarely is the shell crushed by the jaws.

Coloration in life: Breeding males. Ground colour dark grey-green or blue-grey, lighter or yellowish ventrally; a suffused coppery sheen on the flanks and ventral aspects of the operculum. Dorsal fin black basally, becoming slate-coloured distally; lappets red; red spots, often coalesced, between the soft rays. Anal dark with a red flush; ocelli yellow. Caudal dark grey proximally, lighter distally, and with an overall orange-red flush. Pelvics black laterally, orange-red medially. *Non-breeding males* have similar coloration except that the copper flush is absent and other bright colours are less intense. *Females and immature males.* Ground colour golden-green, shading to pearly-white ventrally. All fins yellow-green.

In both sexes there may develop after death a dark longitudinal band running mid-laterally from the eye to the dorsal fin base, a second band running dorso-laterally approximately along the upper lateral-line, and 6–10 narrow transverse bars across the flanks. In life these markings are rarely discernible.

Amongst females a second type of coloration is known. This takes the form of irregular black blotches on a yellow ground and is identical with the *bicolor* pattern

described for certain female *Macrolepurodus bicolor*, *Hoplotilapia retrodens*, and *Haplochromis nigricans* (Greenwood, 1956a and b).

Since collectors show some predilection for fishes with a striking colour pattern, it is difficult to obtain accurate frequency estimates for the *bicolor* pattern. In the present sample, 25 per cent of females are *bicolor*. As most specimens were obtained by collectors aware of possible biasing factors, this figure may be accepted as fairly reliable. No male *bicolor* variants have yet been recorded. Thus, the incidence of *bicolor* variants seems sufficiently high to recognize the phenomenon as sex-limited polychromatism, and not merely the maintenance of an atypical genotype by recurrent mutation. Aberrantly coloured females were found in most localities. None exhibits a pattern intergrading with that usual for females.

Sex-limited polychromatism involving the same phenotypic expression was observed in *M. bicolor* and *Hoplotilapia retrodens* (Greenwood, 1956a). It seems probable that hypotheses regarding its genic basis and evolutionary significance in these species are also applicable to *H. sauvagei*. The possible significance of *bicolor* females as indicating phyletic relationship amongst the various species in which they occur has also been discussed (Greenwood, *op. cit.*). It was concluded that, in general, no reliability could be placed on this character, and that its repeated appearance was probably attributable to the oligophyletic origin of the Lake Victoria species-flock. Nevertheless, it is suggestive that both *H. sauvagei* and *M. bicolor* exhibit "*bicolor*" polychromatism as well as an apparent similarity in fundamental syncranial morphology.

Colour in preserved material: Adult males. Slate-grey to sooty, the longitudinal and transverse banding often obscured. Spinous dorsal fin grey, soft part hyaline but maculate. Anal and caudal hyaline. Pelvics black on the outer half, hyaline mesially. A dark lachrymal stripe and two bars across the snout are often present. *Females and immature males.* Ground colour variable, from silver-grey to brownish. Banding, as described above, usually developed. All fins hyaline, the soft dorsal and upper half of the caudal, maculate.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. Restricted to littoral zones where the bottom is hard (sand or shingle); the species is especially common over exposed sandy beaches.

Food. The gut contents of forty-five fishes from various localities indicate that *H. sauvagei* feed mainly on Gastropoda (f.19), bottom deposits, which included insect larvae, Copepoda and diatoms (f.19), and Insecta (chiefly larval boring may-flies, *Povilla adusta* Navás) (f.4). No fragments of snail shell were observed, although opercula occurred frequently in the stomach and intestine (see also p. 79).

Breeding. Spawning sites and behaviour are unknown. In many localities, sexually active and quiescent fishes, and brooding females occur together.

The smallest adult fish was a female 72 mm. S.L. All specimens over 80 mm. were adult. No difference was detected in the sizes of adult males and females.

Diagnosis. *H. sauvagei* is distinguished from other *Haplochromis* in Lake Victoria by combinations of the following characters: lips thickened; outer teeth with strongly recurved tips; usually more than three inner rows of teeth in the upper jaw (mode 4). The species closely resembles *H. prodromus*, from which it may be

separated by its slightly thinner lips and smaller adult size. In life, male breeding coloration serves to separate the two species.

Affinities. Similarity in the skull architecture and the dentition of *H. sauvagei* and *H. prodromus* suggest a phyletic relationship between the species. Consequent upon these anatomical similarities, the species show a close parallel in their feeding habits and food preferences, although in this respect *H. sauvagei* may be considered less specialized than *H. prodromus*.

Study material and distribution records

Museum and Reg. No.				Locality.	Collector.
<i>Uganda</i>					
B.M. (N.H.)	1908.5.30.365-366	(as <i>Paratilapia granti</i>)		Bunjako	. Degen.
B.M. (N.H.)	1906.5.30.371-372	(as <i>P. granti</i>)	.	Bugonga (Entebbe)	. "
B.M. (N.H.)	1906.5.30.413	.	.	Sesse Is.	. Bayon.
" "	1911.3.3.27	.	.	"	. "
" "	1909.3.29.9	.	.	"	. "
(all as <i>P. bicolor</i>)					
B.M. (N.H.)	1909.5.11.11	.	.	"	. "
" "	1906.5.30.374-377	.	.	Bunjako	. Degen.
" "	1956.9.17.1	(See Text-fig. 1)	.	Entebbe, Airport beach	E.A.F.R.O.
" "	1956.10.9.1-25	.	.	" "	. "
" "	" " " 26-30	.	.	Entebbe, harbour	. "
" "	" " " 31-34	.	.	Bugungu (Napoleon Gulf)	. "
" "	" " " 35-36, 201	.	.	Jinja pier	. "
" "	" " " 37-40	.	.	Shore opposite Kirinya Point (Napoleon Gulf)	. "
" "	" " " 41	.	.	Kirinya Point	. "
" "	" " " 42	.	.	Old Bukakata	. "
" "	" " " 43	.	.	Katebo	. "
<i>Tanganyika Territory</i>					
" "	" " " 44	.	.	Mwanza	. "
" "	" " " 45-72	.	.	Majita	. "
" "	" " " 73	.	.	Ukerewe Is.	. "
" "	" " " 74-75	.	.	Bukoba	. "
<i>Kenya</i>					
" "	" " " 76	.	.	Kisumu	. "
" "	" " " 77-80	.	.	Kamaringa (Kavirondo Gulf)	. "
" "	" " " 81	.	.	Kach Bay (Kavirondo Gulf)	. "
" "	" " " 82	.	.	Open water 5 miles N. of Kendu (Kavirondo Gulf)	. "
" "	" " " 83	.	.	Rusinga Island	. "

***Haplochromis prodromus* Trewavas, 1935**
(Text-figs. 2 and 3)

Paratilapia retrodens (part), Boulenger, 1915, *Cat. Afr. Fish.*, 3, 235.

Haplochromis ishmaeli (part), Boulenger, 1915, *op. cit.*, 293.

Haplochromis annectens Regan 1922 (nec. *Cyrtocara annectens* Regan, 1921), *Proc. zool. Soc. Lond.*, 1922, fig. 2.

Description. Based on sixty-two specimens (including the holotype), 68–130 mm. S.L. None of the morphometric characters studied shows allometry with standard length.

In its general appearance *H. prodromus* closely resembles *H. sauvagei*, from which species it is distinguished by its thicker lips, slightly deeper cheek and larger adult size.

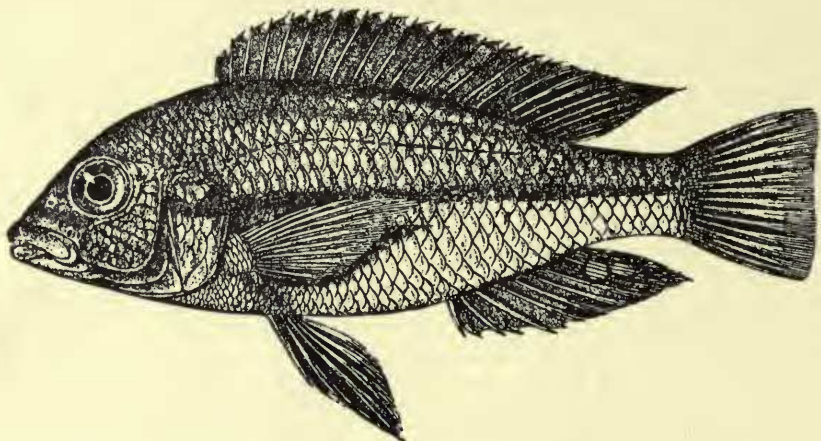


FIG. 2. *Haplochromis prodromus*, ♂, holotype (from Regan, the cichlid fishes of Lake Victoria, *Proc. Zool. Soc.*, 1922, 168, fig. 2).

Depth of body 32.8–40.0 ($M = 36.2$); length of head 29.4–33.6 ($M = 31.5$) per cent of standard length. Dorsal head profile somewhat variable, but always curved; strongly decurved in some large individuals, less so in smaller fishes (70–75 mm. S.L.).

Preorbital depth 14.0–19.1 ($M = 15.8$) per cent head length; least interorbital width 24.0–31.3 ($M = 28.1$) per cent. Snout as broad as or slightly broader than long, rarely longer than broad, its length 27.5–36.8 ($M = 32.7$) per cent of head; eye diameter 25.8–33.3 ($M = 27.8$); cheek 22.0–30.5 ($M = 26.7$) per cent.

Caudal peduncle 12.6–18.1 per cent of standard length, its length 1.0–1.7 (mode 1.3) times its depth.

Mouth horizontal; posterior maxillary tip reaching or almost reaching the vertical to the anterior orbital margin. Lips thickened; the depth of the upper lip, measured mid-laterally, contained $3-3\frac{1}{3}$ times in eye diameter. Jaws equal anteriorly, or infrequently the lower very slightly shorter; lower jaw 30.5–37.8 ($M = 34.3$) per cent of head length, up to 1.3 (mode 1.1) times as long as broad.

Gill rakers short, 7–9 on the lower limb of the anterior arch.

Scales ctenoid ; lateral line with 30 (f.1), 31 (f.7), 32 (f.16), 33 (f.35) or 34 (f.2) scales ; cheek with 3 or 4 series. 7 or 8 (rarely $6\frac{1}{2}$ or 9) scales between origin of dorsal fin and the lateral line, 7 or 8 (less frequently 9) between pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.7), 25 (f.40) or 26 (f.15) rays, anal with 11 (f.7), 12 (f.47) or 13 (f.8), comprising XV–XVII, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral shorter than the head. Pelvic fins with the first ray produced and of variable posterior extension, but reaching the anal fin in most adult fishes. Caudal sub-truncate.

Lower pharyngeal bone triangular, its dentigerous surface about $1\frac{1}{2}$ times as broad as long ; pharyngeal teeth slender and cuspidate ; those of the median series sometimes enlarged.

Teeth. The dental pattern and tooth form in *H. prodromus* closely resemble those of *H. sauvagei*.

In the outer series of both jaws the teeth have strongly recurved tips and are unequally bicuspid or unicuspid. Bicuspid and weakly bicuspid teeth are the predominating forms in fishes less than 100 mm. S.L. Above this size most teeth are unicuspid. 26–56 (mode 40) outer teeth occur in the upper jaw.

Inner teeth are either tri- or unicuspid, the tricuspid form occurring most frequently in fishes less than 90 mm. S.L. Antero-medially the teeth are arranged in 3–7 (modes 4 and 5) and 3–6 (modes 3 and 4) series in the upper and lower jaws respectively. The posterior medial margin of the upper tooth-band is straight or slightly curved, that of the lower band is distinctly curved (Text-fig. 3).

The dental pattern of the holotype must be considered aberrant ; it is not repeated in any of the sixty-one additional specimens. In the type, some postero-lateral inner teeth are displaced medially from their series, thereby giving a spurious impression of a tooth band widened at that point. There is no increase in the width of the underlying premaxillary alveolar surface, nor is there an increase in the number of tooth rows (see fig. 14 in Regan, 1922). In all other respects the dentition of this specimen agrees closely with those described above.

Syncranium and associated musculature. The neurocranium and premaxilla of *H. prodromus* are virtually identical with those of *H. sauvagei*. The dentary, however, is relatively more massive and the mental profile is almost vertical.

Likewise, the jaw musculature compares closely with that of *H. sauvagei*, except that the *adductor mandibulae* I is somewhat shorter (36–39 per cent head length).

Observations made on the feeding methods of *H. prodromus* kept in aquaria, indicate that snails are removed from their shells in a manner similar to that employed by *Macropleurodon bicolor*. That is, the shell is crushed free by the jaws before ingestion takes place. The species was not seen to lever out the soft parts as is usual with *H. sauvagei*.

Coloration in life : Adult males. Ground colour slaty blue-grey ; a peacock-blue sheen on the belly and ventral flanks. Chest and branchiostegal membrane black, operculum with a golden flush. Very faint indications of a dark mid-lateral stripe and seven transverse bars ; also a faint lachrymal stripe. Dorsal dark, with a deep red flush between both spinous and soft rays ; lappets orange. Anal sooty, ocelli

deep yellow. Caudal sooty, with a faint orange flush along its posterior margin. Pelvics black. *Females and immature males.* Ground colour silver-grey above the mid-lateral stripe and silver below, with a faint peacock-blue flush on the flanks. Transverse barring is indistinct. Dorsal fin dark. Caudal and anal hyaline. Pelvics faintly yellow.

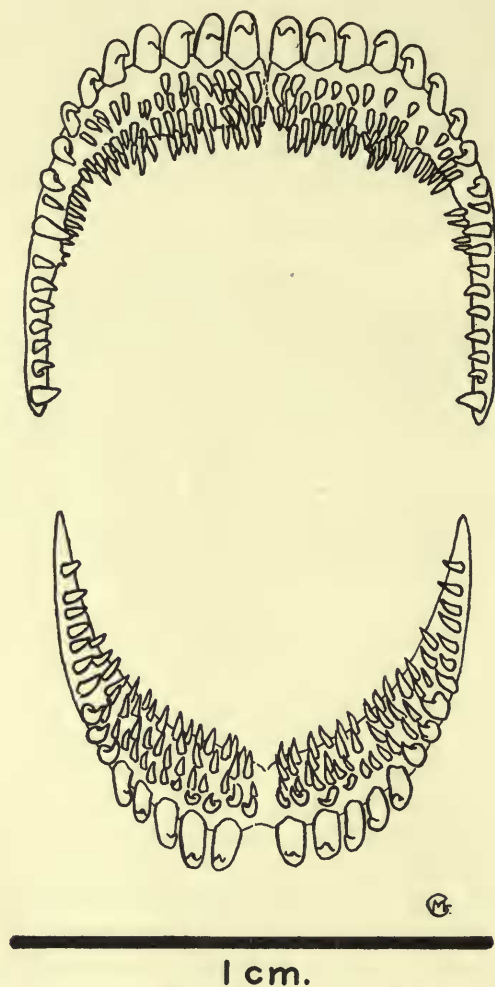


FIG. 3. The premaxillary and mandibular tooth bands in *H. prodromus*.

Colour in preserved material: Adult males. Ground colour dark grey; in some, faint traces of transverse and longitudinal banding. Chest and branchiostegal membrane black. Dorsal, caudal and anal dark, the soft dorsal maculate. Pelvics black. *Females and immature males.* Pale, banding variable but usually a distinct mid-lateral stripe and a faint, more dorsal band running along the upper lateral line; five to nine transverse bars across the flank. All fins hyaline.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. Restricted to littoral zones, particularly where the substrate is hard (sand or shingle) and occurring less frequently over mud. Thus, the habitat of *H. prodromus* broadly overlaps that of *H. sauvagei*. Nevertheless, although biasing factors are introduced by the size selectivity of sampling gear and the limitations imposed by the habitat on the use of certain gear, it seems that *H. sauvagei* occur most frequently over shallow exposed beaches—where *H. prodromus* are less common—and that *H. prodromus* are more abundant in off-shore to deeper waters. This assumption is supported by results obtained when such non-selective collecting methods as explosives were used in both habitats.

Study material and distribution records

Museum and Reg. No.	Locality.	Collector.
<i>Uganda</i>		
B.M. (N.H.) 1907.5.7.78 (holotype <i>H. prodromus</i>)	Buddu coast	. Simon.
" " 1906.5.30.379 (as <i>P. retrodens</i>)	Bunjako	. Degen.
B.M. (N.H.) 1956.10.9 84-97	Jinja	. E.A.F.R.O.
" " " " 98-99	Shore opposite Kirinya Point (Napoleon Gulf)	. "
" " " " 100-105	Beach near Nasu Point (Buvuma Channel)	. "
" " " " 106	Pilkington Bay	. "
" " " " 107	Hannington Bay	. "
" " " " 108-125	Entebbe harbour	. "
" " " " 126	Katebo	. "
" " " " 127-129	Busungwe Bay (Kagera river mouth)	. "
" " " " 130	Dagusi Island	. "
<i>Tanganyika Territory</i>		
" " " " 131-133	Mwanza, Capri Bay	. "
" " " " 134-135	Godziba Island	. "
" " " " 197-199	Majita	. "
<i>Kenya</i>		
" " " " 136-137, 196	Kamaringa (Kaviron-do Gulf)	. "
" " " " 138	Kisumu	. "

Food. Stomach and intestinal contents of seventy-four fishes were examined. Of these, eleven were empty, fifty-seven contained only the remains of Gastropoda, three contained Gastropoda and Insecta, and three yielded unidentifiable sludge. Due to their very fragmentary nature the specific identification of molluscan remains was difficult; where identification was possible the genus *Bellamya* predominated. As many as twenty-two snail opercula were recorded from the intestine of a single fish, although the modal estimated number of snails per individual was about four.

Breeding. Sexually active and quiescent individuals were associated in all localities, but no data were collected on breeding sites or spawning behaviour. Only one female was found carrying larvae in the buccal cavity. There is apparently no sex-correlated adult size difference in this species; the smallest sexually active individual was a male 102 mm. long.

Diagnosis. The same character complex serves to separate *H. sauvagei* and *H. prodromus* from the other *Haplochromis* of Lake Victoria. *H. prodromus* is distinguished from *H. sauvagei* by its larger adult size, thicker lips, slightly deeper cheek, and, in life, by male breeding coloration.

Affinities. The apparent phyletic relationship between *H. prodromus* and *H. sauvagei* on the one hand, and the more specialized *Macropheurodus bicolor* on the other, has been discussed above and elsewhere (Greenwood 1956a). In the latter paper, it was shown that Regan's suggested relationship between *H. prodromus* and *Platytaeniodus degeni* Blgr. can no longer be considered valid. Regan's views were based on the type and then unique specimen of *H. prodromus* whose dental pattern is aberrant. In any case, the posterior widening of the premaxillary dental surface is apparent and not actual in this fish, whereas in *P. degeni* the premaxilla undergoes a localized but distinct broadening during post-larval ontogeny.

***Haplochromis granti* Boulenger, 1906**
(Text-figs. 4 and 5)

Paratilapia granti (part), Boulenger, 1915, *Cat. Afr. Fish.*, 3, 342, Fig. 231.
Haplochromis sauvagei (part), Regan, 1922, *Proc. zool. Soc., Lond.*, 167.

In Regan's revision of the Lake Victoria Cichlidae (*ibid.*, 1922), *H. granti* was treated as a synonym of *H. sauvagei*. After comparing the type with other specimens now available, I conclude that the two species should be regarded as distinct. This conclusion is supported by field observations. Both species have in common the "*sauvagei*" group characters of broad inner tooth bands, outer teeth with strongly recurved tips, and thickened lips. But they differ considerably in gross morphology and in certain details of dental pattern. The holotype of *H. granti* (figured in Boulenger, 1915) does not present a specifically typical appearance. However, its dental pattern indicates conspecificity with the specimens here described as *H. granti*. Furthermore, in the type, characters which contribute to gross morphology, for instance the form of the dentary and the head shape, intergrade with those of other specimens possessing a more typical facies.

One rather damaged specimen (B.M. (N.H.) Reg. No. 1911.3.3.28), identified by Boulenger as *Paratilapia retrodens* and later by Regan as *H. sauvagei*, should probably be referred to *H. granti*. Because of this uncertainty *P. retrodens* is not included in the revised synonymy of *H. granti*.

Description.—Based on the type, two paratypes and twenty-six additional specimens in the size range 70–122 mm. S.L. No clear-cut allometry with standard length was observed in the morphometric characters listed below.

Depth of body 32.7–39.3 ($M = 35.4$); length of head 28.8–33.3 ($M = 31.5$) per

cent of standard length. Dorsal head profile slightly curved, or, less frequently, straight and gently to steeply sloping.

Preorbital depth 15.3–19.0 (13.3 in the smallest specimen) ($M = 17.1$) per cent of head length; least interorbital width 25.0–32.8 ($M = 28.6$) per cent. Snout as broad as or slightly broader than long, its length 29.0–36.0 ($M = 31.6$) per cent of head; eye diameter 25.0–31.0 ($M = 27.5$); depth of cheek 22.0–30.6 ($M = 26.8$) per cent.

Caudal peduncle 13.6–19.0 per cent of standard length, 1.2–1.7 times as long as deep.

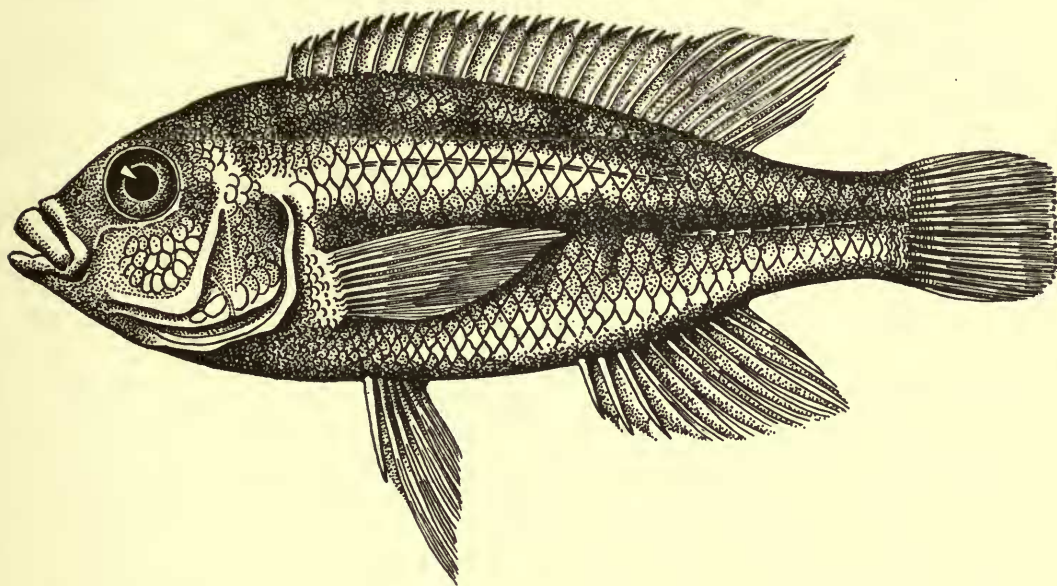


FIG. 4. *Haplochromis granti*, ♀, B.M. (N.H.) 1956.9.17.2. Drawn by Miss L. Buswell.

Mouth usually somewhat oblique; posterior maxillary tip almost reaching the vertical to the anterior orbital margin, or occasionally reaching this line. Lips thick, sub-equally developed in a few specimens (e.g. the type), but the upper lip clearly thicker than the lower in most. Jaws equal anteriorly, or the lower jaw slightly projecting, its length 22.2–30.6 ($M = 26.8$) per cent of head length and 1.0–1.5 (mode 1.3) times its width.

The oblique mouth and unequally thickened lips give an appearance of deformity to many specimens. This impression is apparently misleading since there is no indication of any impairment to the efficiency of the jaw mechanism, either as a mechanical unit or in relation to feeding habits.

Gill-rakers short, 7–9 on the lower limb of the first arch.

Scales ctenoid, lateral line with 32 (f.9), 33 (f.11), or 34 (f.9) scales; cheek with 3 or 4 (in one specimen 2) series; 7 or 8 scales between origin of dorsal fin and lateral line; 7 or 8 (rarely 9) between pectoral and pelvic fin bases.

Fins. Dorsal with 25 (f.11), 26 (f.17) or 27 (f.1) rays; anal 11 (f.7) or 12 (f.21), comprising XV–XVII, 9 or 10 and III, 8 or 9 spinous and branched rays for the fins respectively. In one specimen the anal fin had been damaged and subsequently healed irregularly, giving II, 10 rays. Pectoral shorter than the head, except in two specimens where it is of the same length. Pelvic fins extending to the vent in immature fishes and to the anal fin in adults; the first ray is proportionately more produced in sexually active males. Caudal fin truncate or sub-truncate.

Lower pharyngeal bone triangular, its dentigerous surface $1\frac{1}{3}$ – $1\frac{1}{4}$ times as broad as long; pharyngeal teeth similar to those of *H. prodromus*.

Teeth. In the outer series of both jaws, the teeth are similar to those of *H. prodromus* and *H. sauvagei*; that is, unicuspid with strongly recurved tips. A few specimens—all below 90 mm. S.L.—have some bicuspid teeth situated postero-laterally in both jaws. There are 28–46 (mode, ill defined: 36) outer teeth in the upper jaw.

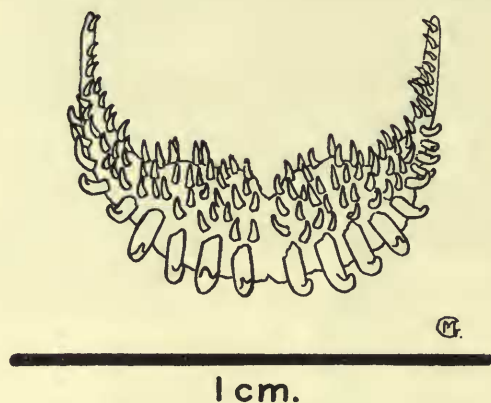


FIG. 5. Mandibular tooth band in *H. granti*.

The inner series are composed of tricuspid teeth in most fishes below 90 mm. and of unicuspid teeth in larger specimens. An admixture of both types is known from three fishes. The teeth are arranged in 2–6 (mode 4) rows in both jaws, but narrow to single series laterally. In many specimens the lower tooth band is wider than the upper; antero-medially, the posterior margin of this band is straight or very gently curved, thus contrasting with the lower series in *H. sauvagei* and *H. prodromus*, where the margin is clearly curved (Text-fig. 5).

Syncranium and associated musculature. The preorbital face of the neurocranium is intermediate in form between that of *H. sauvagei* and the generalized *Haplochromis* type. Greatest departure from the condition observed in *H. sauvagei* and *H. prodromus* is seen in the maxilla, which in *H. granti* is shorter and more bowed in its long axis. Also, the inner face of the posterior limb is markedly concave, which results in the outer face appearing more bullate than in other members of the “*sauvagei*” group. The dentary resembles that of *H. sauvagei* but differs in its less rounded, more angular, anterior outline.

Shortage of material allowed only two dissections of head musculature to be made. The major muscles are distributed as in *H. prodromus* and *H. sauvagei* but the origin of the *adductor mandibulae* I is deeper and more fan-shaped in *H. granti*. In the two specimens dissected, the length of this muscle (42 and 43 per cent of head) is somewhat greater than in *H. prodromus* but equal to that in *H. sauvagei*.

Coloration in life: Adult males. Ground colour light blue-grey; branchiostegal membrane dusky, especially between the rami of the lower jaw. Dorsal fin blue-grey, darkest on the proximal third; lappets orange-red, as are the spots and streaks between the soft rays. Caudal blue-grey, darker on the proximal half; margin outlined in red; orange-red spots between the rays. Anal dusky blue-grey, with an overall pink flush; ocelli yellow. Pelvics black, faint pink mesially. *Females and immature males.* Coloration in life unknown.

Colour in preserved material: Adult males. Ground colour grey or brown; branchiostegal membrane dark grey. An intense black mid-lateral stripe and often traces of a lachrymal stripe and 5-7 vertical bars across the flanks. Dorsal, caudal and anal fins hyaline or dusky; pelvics black. *Females and immature males.* Ground colour silver-white, darkest dorsally. An intense mid-lateral stripe and often faint indications of an interrupted upper band running between the dorsal fin base and the upper lateral line. Seven to nine faint transverse bars are usually present on the flanks and caudal peduncle; no lachrymal stripe. All fins hyaline.

Distribution. Confined to Lake Victoria.

Ecology: Habitat. Too few records are available to permit generalization on the habitat preferences of *H. granti*. The twenty-six specimens whose habitat had been recorded were caught in littoral zones and in water less than forty feet deep. Most localities represented in the collection can be classified either as sandy beaches on exposed shores or as exposed coastlines with a hard substrate. The few remaining localities are sheltered bays where the bottom is composed of organic mud.

Food. Twelve of the twenty-six fishes examined contained ingested material in the stomach or intestine. In each case only the soft parts of Gastropoda were found, except for some Lamellibranchiata shell fragments in one individual. From these admittedly few observations it is inferred that *H. granti* feed in a manner similar to that observed for *H. prodromus* and *H. sauvagei*.

Breeding. There is no information on any aspect of the breeding behaviour in this species; all specimens below 90 mm. S.L. were immature.

Diagnosis. *Haplochromis granti* differs from other Lake Victoria *Haplochromis* in possessing broad bands of inner teeth (2-6, mode 4, series) in both jaws and by its unequally thickened lips, the upper usually thicker than the lower. This latter character, together with the oblique mouth and straight posterior margin to the inner tooth band of the lower jaw, serves to distinguish *H. granti* from *H. prodromus* and *H. sauvagei*.

Affinities. By virtue of its dentition, *H. granti* must be included in the *H. sauvagei*-*H. prodromus* species-group. Other characters probably associated with dentition, such as the shape of the premaxilla and dentary, are closely similar in all three species. But, despite resemblances in these dental and osteological characters, and in the associated musculature, the neurocranial morphology of *H. granti* has not

departed so radically from the generalized *Haplochromis* type. Morphologically speaking, the relationship between *H. sawagei* and *H. prodromus* is directly linear, whilst that of *H. granti* is somewhat divergent but with a parallel trophic trend.

Study material and distribution records

Museum and Reg. No.	Locality.	Collector.
<i>Uganda</i>		
B.M. (N.H.) 1903.5.30.367 (holotype <i>P. granti</i>)	Bunjako	Degen.
B.M. (N.H.) 1903.5.30.368-369 (paratypes <i>P. granti</i>)	"	"
B.M. (N.H.) 1956.10.9.139	Bay opposite Kirinya Point (Napoleon Gulf)	E.A.F.R.O.
" " " " 140-141	Bugungu (Napoleon Gulf)	"
" " " " 142-144	Beach nr. Nasu Point (Buvuma Channel)	"
E. African Fisheries Res. Lab. Jinja	Pilkington Bay	"
B.M. (N.H.) 1956.10.9.145-147	Thruston Bay	"
" " 1956.9.17.2	Ekunu Bay	"
" " 1956.10.9.148-152	Entebbe, harbour	"
" " " " 153	Near Busungwe Is.	"
" " " " 154	Busungwe Bay (Kagera river mouth)	"
" " " " 155-157	Beach near Grant Bay	"
" " " " 200	Buka Bay	"
<i>Kenya</i>		
" " " " 158	Kisumu	"
<i>Tanganyika</i>		
" " " " 159	Ukerewe Is.	"
" " " " 160-163	Majita	"

Haplochromis xenognathus sp. nov.

(Text-figs. 6 and 7)

The high intra-specific variability of *H. xenognathus* makes this species of particular interest when considering the evolution of monotypic cichlid genera. Some of the more aberrant specimens, if studied in isolation, might well be given a status equal with the monotypic genera recognized at present. Less extreme individuals, on the other hand are not immediately distinguishable from *H. sawagei*.

The modal type tooth-pattern and the usual arrangement of the jaws are, however, unlike those of other species in the "*sawagei*" group (Text fig. 7). I am led to include *H. xenognathus* in this group because of its "*sawagei*"-like tooth form and the multiseriata dental pattern.

The sample provides sufficient intra-specific variation to indicate morphological

stages through which the typical specific facies may have passed in its evolution from a form similar to the extant *H. sauvagei*.

Type specimen. A male, 91 + 19 mm.; from Entebbe harbour.

Description. Based on thirty-five specimens 80–113 mm. S.L.

Depth of body 31.2–38.0 ($M = 34.8$); length of head 29.2–35.4 ($M = 33.1$) per cent of standard length. Dorsal head profile usually straight and somewhat steeply sloping; curved in a few specimens.

Preorbital depth 16.0–20.7 ($M = 17.7$) per cent head length; least interorbital width 23.5–29.0 ($M = 26.8$) per cent. Snout from $1\frac{1}{5}$ – $1\frac{1}{3}$ longer than broad, its length 31.8–37.8 ($M = 35.2$) per cent of head; eye 23.2–28.7 ($M = 26.0$); depth of cheek 23.2–28.7 ($M = 26.0$) per cent.

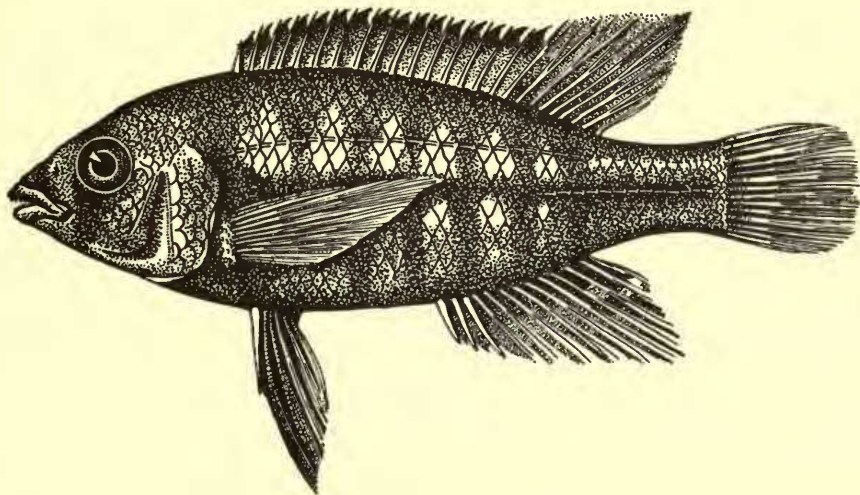


FIG. 6. *Haplochromis xenognathus*, ♂, holotype, B.M. (N.H.) 1956.9.17.3.
Drawn by Miss L. Buswell.

Caudal peduncle 13.8–19.0 ($M = 15.9$) per cent of standard length; 1.1–1.7 (mode 1.4) times as long as deep.

Mouth horizontal, the posterior maxillary tip reaching, or almost reaching, the vertical to the anterior orbital margin; lips slightly thickened. The lower jar is clearly shorter than the upper in 74 per cent of the specimens examined and subequal to the upper in 26 per cent. Even in this latter group the outermost teeth of the lower jaw occlude behind the equivalent upper jaw series. Lower jaw 32.0–38.0 ($M = 34.5$) per cent of head, and 1.1–1.8 (mode 1.4) times as long as broad.

Gill rakers short, 7–9 (rarely 10) on the lower limb of the first arch.

Scales ctenoid; lateral line with 31 (f.4), 32 (f.14), 33 (f.11), 34 (f.4) or 35 (f.2) scales; cheek with 3 or 4 (rarely 2 or 5) series; 6 or 7 (less frequently 8) scales between origin of dorsal fin and lateral line; 7 or 8 (rarely 6 or 9) between pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.13), 25 (f.19), or 26 (f.3) rays ; anal with 11 (f.9), 12 (f.24) or 13 (f.1). One specimen has only two spines, giving a total count of 10 rays. The spinous and branched ray counts for the fins are XV-XVII, 8-10 and III, 8-10. Pectoral fins shorter than the head. Pelvic fins with first ray produced, extending to the anterior part of the anal fin in females and more posteriorly in adult males. Caudal truncate.

Lower pharyngeal bone triangular, its dentigerous surface $1\frac{1}{3}$ - $1\frac{1}{2}$ times as broad as long. The pharyngeal teeth are slender and bicuspid, those of the median series not noticeably enlarged. In one specimen, the lower pharyngeal bone is stout, the toothed surface slightly longer than broad and the median teeth enlarged and molariform ; this fish also shows a somewhat atypical oral dentition, in that the teeth are bluntly cuspidate.

Teeth. Except in the smallest specimen, unicuspid teeth predominate in the outer series, but some weakly bicuspid teeth do occur postero-laterally in both jaws of large fishes. In the smallest specimen, the entire outermost series is composed of bicuspid teeth.

The outer teeth, like those of *H. sauvagei* and other species of the group, are relatively stout and have strongly recurved tips. In the lower jaw, the anterior teeth are implanted at an acute angle, so that their necks lie almost horizontally ; but recurvature of the crown is such that the tip points almost vertically upwards (Text-fig. 8). There are from 32-52 (mode 44) outer teeth in the upper jaw.

Teeth forming the inner series are small and either unicuspid or weakly tricuspid. Considerable variation exists in the number of inner rows. In general, teeth are disposed in a broad crescent which narrows abruptly at a point almost mid-way along the premaxillary limb. Thereafter, there is a single inner row. The antero-medial depth of this band varies with the number of tooth rows, of which there are from 3-9 in both jaws (modes 7 and 5 for the upper and lower jaws respectively). In fishes with markedly disparate jaws, the most posterior inner teeth of the dentary do not occlude with the upper series.

The toothed surface of the dentary is often slightly convex, so that when viewed laterally several points on the inner band are higher than the crowns of the outer teeth (Text-fig. 8).

Fishes with narrow tooth bands in both jaws have a dental pattern closely resembling that of *H. sauvagei* ; the resemblance to this species is enhanced by the sub-equal jaws of these specimens. In contradistinction, other *H. xenognathus* with sub-equal jaws have a broad and specifically typical tooth pattern.

Syncranium and associated musculature. The neurocranium of *H. xenognathus* is identical with that of *H. granti*. The shape of the premaxilla varies slightly in relation to the number of inner tooth rows, but is otherwise comparable with the premaxilla of *H. sauvagei*. Likewise the dentary is similar in the two species, except that the dentigerous surface is inclined forwards and downwards in *H. xenognathus*. Perhaps the most characteristic appearance of this bone is imparted by the almost horizontally implanted anterior teeth.

A syncranial skeleton prepared from a specimen with *H. sauvagei*-like facies did

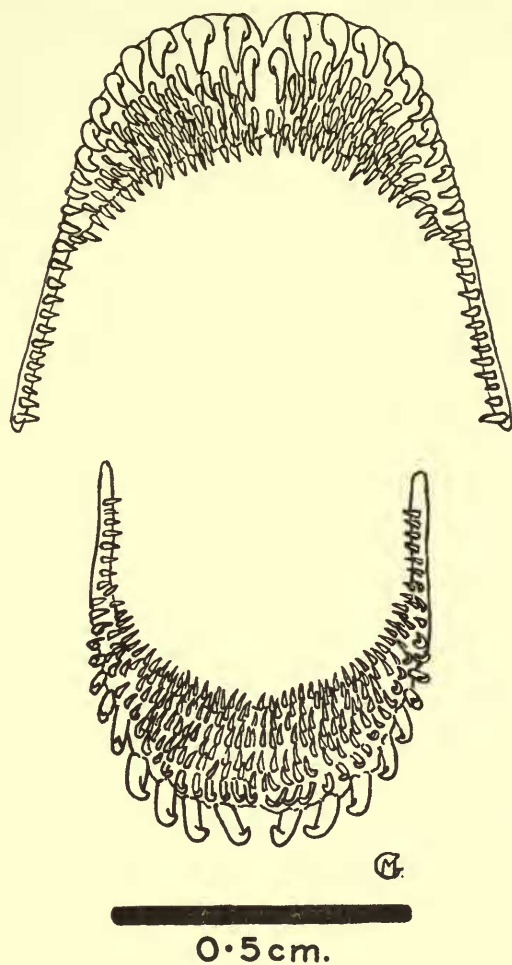


FIG. 7. Premaxillary and mandibular tooth bands in *H. xenognathus*.

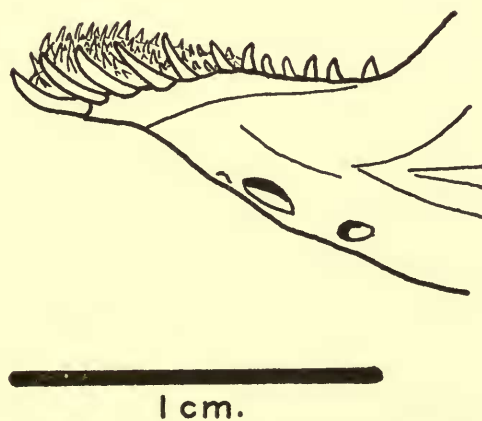


FIG. 8. Lateral view of the anterior part of the dentary of *H. xenognathus*.

not differ, beyond the limits of individual variability, from that of a typical specimen and was clearly distinguishable from that of *H. sauvagei*.

Head musculature in *H. xenognathus* is similar to that of *H. sauvagei* and *H. prodromus*. The *adductor mandibulae* I is shorter than in the former species, but is equal to that of the latter (33.2–39.4 per cent of head).

Coloration in life: Adult males. Ground colour dark bronze dorsally, shading to grey-bronze ventrally: cheek and operculum with a distinct bronze sheen; chest and branchiostegal membrane bluish-grey. Dorsal fin sooty, with red streaks between the soft rays; lappets red. Caudal dark, upper half with red spots, lower half flushed with red. Anal clouded; ocelli yellow. Ventrals sooty, the first ray bluish-white. Live coloration of *immature males* is unknown. *Females.* Ground colour as in males, but the branchiostegal membrane greyish. Dorsal fin with red lappets but lacking the red streaks. Caudal dark yellow ventrally, lighter and maculate above. Anal and ventral fins dark olive-yellow, the first pelvic ray bluish-white.

Colour in preserved material: Breeding males. Dark grey, the flank with a faint coppery sheen; a distinct lachrymal stripe. In some specimens five transverse bars may be discerned on the flanks. Dorsal, caudal and anal fins grey, the upper third of the caudal maculate. Pelvic fins black. *Non-breeding and immature males.* Ground colour silver-grey; 7–9 distinct transverse bars. Fins as above. *Females.* As for non-breeding males, except that the pelvics are colourless. In some specimens there is a fairly distinct mid-lateral stripe.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. The few and scattered records indicate that *H. xenognathus* is confined to littoral zones where the substrate is hard. Most specimens in the collection were obtained from seine nets operated over exposed sandy beaches.

Food. Seventeen of twenty-three fishes examined contained ingested material in the stomach or intestine: in ten, only the soft parts of Gastropoda were found; in three, Insecta (chironomid and ephemerid larvae); in two, bottom detritus (sand-grains and plant tissue); and in three, unidentifiable sludge.

Although no observations have been made on living fishes, the presence of gastropod remains without shells suggests that the feeding methods of *H. xenognathus* are like those of *H. sauvagei*, *H. prodromus* and *H. granti*.

Breeding. No information is available. The smallest sexually mature fish was a female 87 mm. S.L.

Diagnosis. *Haplochromis xenognathus* may be distinguished from other species of the genus by the following characters: outer teeth with strongly recurved tips, those of the lower jaw implanted horizontally or almost so; inner teeth in the upper jaw arranged in a broad, crescentic band (3–7, mode 5 series); lower jaw usually much shorter than the upper and also with broad bands of teeth (3–9, mode 5, inner series). Some individuals closely resemble *H. sauvagei* both in gross morphology and in details of dentition, but may be distinguished by the peculiar implantation of their anterior lower teeth and by having a slightly narrower and longer snout; in life the coloration of both sexes is diagnostic.

Affinities. In many respects the species has departed considerably from the basic

"*sauvagei*" type as represented by the nominate species. Yet, it is apparently with *H. sauvagei* that *H. xenognathus* shows greatest morphological affinity. The resemblance is most clearly seen in the least typical members of *H. xenognathus*, but is obscured in other forms. These latter individuals seem to indicate that if future evolution in *H. xenognathus* is continued along such lines and is coupled with a reduction in morphological variation, then the species could acquire a status equivalent to the monotypic genera recognized at present.

Study material and distribution records

	Museum and Reg. No.		Locality.	Collector.
B.M. (N.H.)	1956.10.9.164-167	. . .	Jinja	E.A.F.R.O.
" "	" " " 168	. . .	Bay opposite Kirinya Point (Napoleon Gulf)	"
" "	" " " 169	. . .	Beach nr. Nasu Point (Buvuma Channel)	"
" "	" " " 170	. . .	Hannington Bay	"
" "	1956.9.17.3 (type)	. . .	Entebbe, harbour	"
" "	1956.10.9.171-173	. . .	" "	"
" "	" " " 174	. . .	Entebbe, Airport beach	"
" "	" " " 175	. . .	Bugonga, Entebbe peninsula	"
" "	" " " 176-177	. . .	Katebo	"
" "	" " " 178-182	. . .	Beach south of Busungwe (Kagera river mouth)	"

Tanganyika

" "	" " " 183	. . .	Bukoba	"
" "	" " " 184-191	. . .	Majita	"
" "	" " " 192-195	. . .	Mwanza, Capri Bay	"

DISCUSSION

In an adaptively multi-radiate species-flock, the differentiation of true phyletic relationship from parallel trends is difficult, particularly when the flock, like that of Lake Victoria, is oligophyletic in origin. It has been noticed, however, that in many adaptive sub-groups some species show greater morphological affinity with one another than with other members. This I interpret as indicating that both lineal descent and parallel evolution have contributed to the origins of the groups.

The remarkable uniformity of the distinctively shaped outer teeth in all four members of the "*sauvagei*" complex probably indicates a monophyletic origin for the group. Their multiseriate dentition, on the other hand, cannot be considered of value in indicating phylogeny. Broad tooth-bands have evolved in several other and unrelated species, for example, the algal-grazers *H. nigricans* and *H. nuchi-squamulatus*, and in certain monotypic genera.

As an ecologically defined group, the "*sauvagei*" complex exhibits considerable variation in species morphology. There are three distinctive forms, represented by

H. sauvagei and *H. prodromus*, *H. granti*, and *H. xenognathus*. The two first-mentioned species must be considered nearer the generalized type and the two latter as showing progressive but independent divergence.

When discussing the evolution of *Macropleurodus bicolor*, I drew attention to the possible relationship between this species and *Haplochromis prodromus* (Greenwood, 1956a). No conclusion can be reached at present, but the prospective adaptational significance of a "*prodromus*" type cranial anatomy in the evolution of *M. bicolor* cannot be disregarded. That both species should have almost identical feeding habits would seem to lend additional weight to this argument.

Morphological and ecological differences between *H. prodromus* and *H. sauvagei* are of the slightest order. If their lineal relationship can be accepted, one is tempted to consider the species in an ancestor-descendant category. In all probability, present-day *H. sauvagei* differ genotypically and even phenotypically from the presumed ancestral type, yet, despite these limitations, it is difficult to imagine a species more similar to *H. prodromus*. Several other such *Haplochromis* species-pairs are known from Lake Victoria. Each, except for their temporal coexistence, would fulfil the palaeontological requirements for ancestor-descendant relationship. Indeed, coexistence, even within one habitat, of species which could be lineally derived appears to be a major feature of the Lake Victoria *Haplochromis* species-flock. The Lake's geological history provides a possible explanation of this phenomenon (Brooks, 1950; Greenwood, 1951). During the inter-Pluvial periods of the Pleistocene, Lake Victoria was probably reduced to a series of small lakes and swamps. Under such conditions a species would be isolated into several discontinuous groups. If some surviving populations underwent genic reorganization as a result of isolation, or of increased selection pressure, it is possible that they might retain their discreteness if brought into contact with the parental stocks when the lakes were joined during the succeeding Pluvial period. That the derived and parental species were able to coexist even when their ecological requirements were similar, seems to indicate drastically reduced selection pressure.

The third member of the "*sauvagei*" group, *H. granti*, is unlike either *H. sauvagei* or *H. prodromus*. However, the differences lie in characters which could be derived by heterogonic growth of certain cranial parts from a species less differentiated than *H. sauvagei*, but possessing the group dental characters.

From an evolutionary viewpoint, *H. xenognathus* is undoubtedly the most interesting species. When the first few specimens came to my notice, I considered them to be members of a distinct and apparently monotypic genus. The degree of morphological differentiation of this supposedly new genus was at least equal to that of *Hoplotilapia retrodus* Hilg. When more specimens were collected, however, it was obvious that the species was extremely variable and should be retained within the genus *Haplochromis*. The less typical specimens differed only slightly from *H. sauvagei*, whilst the typical fishes were clearly distinct from that species. Thus, it seems legitimate to look upon *H. xenognathus* as an example of a stage through which species might pass in the evolution of a genus.

Ecologically, the "*sauvagei*" group has entered an adaptive zone unique for *Haplochromis*, but occupied by two monotypic genera, *Macropleurodus bicolor* and

Hoplotilapia retrodens. All other known predominantly mollusc-eating *Haplochromis* species crush their prey by means of hypertrophied pharyngeal bones and dentition.

If, in conclusion, one considers the morphological and consequent ecological adaptations of the *H. sauvagei* group, the impression is gained of a species-complex partially advanced on the path of trophic specialization. From its present peak it could supply, and may even have supplied, raw material for further specialization.

SUMMARY

1. *Haplochromis sauvagei* (Pfeffer) 1896, and *H. prodromus* Trewavas 1935, are re-described.

2. The species *H. granti* Blgr. 1906, previously synonymized with *H. sauvagei*, is reinstated.

3. A new species, *Haplochromis xenognathus*, is described.

4. Data are given on the ecology of all four species.

5. Sex-limited polychromatism, involving a piebald female coloration, is described for *H. sauvagei*.

6. The evolutionary status of the species is discussed.

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ACKNOWLEDGMENTS

I wish to express my gratitude to the Trustees of the British Museum (Natural History) for the numerous facilities afforded me in their museum; to Dr. Ethelwynn Trewavas for her constant help and for reading the manuscript of this paper; and to my colleague Dr. Philip S. Corbet who identified the insects recorded from stomach contents.